

Critical behavior in an evolutionary model of altruistic behavior with social structure

Víctor M. Eguíluz*

*Instituto Mediterráneo de Estudios Avanzados IMEDEA
(CSIC-UIB), E-07122 Palma de Mallorca, Spain*

Claudio J. Tessone†

*Chair of Systems Design, ETH Zürich,
Kreuzplatz 5, CH-8032 Zürich, Switzerland and
Instituto Mediterráneo de Estudios Avanzados IMEDEA
(CSIC-UIB), E-07122 Palma de Mallorca, Spain*

(Dated: May 20, 2009)

Experimental studies have shown the ubiquity of altruistic behavior in human societies. The social structure is a fundamental ingredient to understand the degree of altruism displayed by the members of a society, in contrast to individual-based features, like for example age or gender, which have been shown not to be relevant to determine the level of altruistic behavior. We explore an evolutionary model aiming to delve how altruistic behavior is affected by social structure. We investigate the dynamics of interacting individuals playing the Ultimatum Game with their neighbors given by a social network of interaction. We show that a population self-organizes in a critical state where the degree of altruism depends on the topology characterizing the social structure. In general, individuals offering large shares but in turn accepting large shares, are removed from the population. In heterogeneous social networks, individuals offering intermediate shares are strongly selected in contrast to random homogeneous networks where a broad range of offers, below a critical one, is similarly present in the population.

PACS numbers:

*Electronic address: victor@imedea.uib.es; URL: <http://www.imedea.uib.es/~victor>

I. INTRODUCTION

How cooperative behavior emerges among interacting individuals is a long-standing problem that has attracted, starting from Darwin, the attention of a large number of researches [8, 11, 29]. In the context of Game Theory, different mechanisms and models have been proposed to explain the observed cooperative behavior, two prominent examples being the Ultimatum Game [12] and the Prisoner's Dilemma [3]. Theoretical studies, have shown that, selection at the individual level, may lead to altruistic behavior [31], in contrast to the general belief that only group selection can give raise to altruism.

Aiming at understanding the mechanisms leading to altruism as the core of cooperative behavior, the Ultimatum Game is one of the paradigmatic theoretical games used to understand their interrelation. The simplicity of this game has allowed to obtain a large set of experimental results that clearly show the presence of altruistic behavior, in the form of *altruistic punishment*. Altruistic punishment, meaning that individuals react to an unfavorable action by an opponent although the punishment is costly for them and yields no material gain, is a key ingredient for the

explanation of cooperation as it emerges if altruistic punishment is possible, while breaks down if it is ruled out [10]. The ultimatum game consists of two agents, who have to share a given amount of money. One of them, the *proposer*, makes an offer on how to share the money to the other agent, the *responder*. The proposer can only make one offer. The responder decides whether he accepts or rejects the offer. If the responder accepts, the money is shared as proposed; otherwise, none of them get anything. Given that a narrowly rational responder would accept no matter what he has been offered –something is better than nothing–, a narrowly rational proposer would offer to the responder the minimum amount. However, real agents behave differently: offers are typically close to a 50-50 ratio and offers below 20% are typically rejected [17, 18, 24].

Recently, an extensive research performed among small societies around the world [16] has shown that social structure is a key element in determining the degree of cooperation among its members [17, 18]. On the one hand, individual-based features seem not to be relevant in order to determine the degree of cooperation. On the other hand, in the Ultimatum Game, the proposals and rejection levels are different depending on the social structure. For example, societies based on cooperation and sharing of food, show

[†]Electronic address: tessonec@ethz.ch;

URL: <http://www.imedeaiuib.es/~tessonec>

higher offering levels. From the theoretical point of view the effect of structured populations in social dilemmas, e.g., the prisoner's dilemma, public good games, or snowdrift games, has been analyzed mainly from the perspective of spatially extended populations [14, 15, 22, 27]. In the simplest case, local interactions are considered in regular lattices where each individual interacts only within its local neighborhood in contrast to global random interactions considered in well mixed populations. However, recent progress in this area has shown that many social and biological interaction networks are not regular, as typically used in theoretical models, but display the small-world behavior and broad degree distributions [1, 2, 13, 23, 28, 33].

The question we address here is precisely how social structure affects the degree of altruistic behavior. This paper is organized as follows: In the next Section we define the evolutionary ultimatum game model in a complex network. In Section III, following the tradition of spatial games, we first consider interactions given by a regular lattice; later extending our analysis to random and small-world networks, which are characterized by single-scale degree distributions; in Section IIIB, we also consider scale-free networks. Finally we discuss our results and draw the conclusions in Section IV.

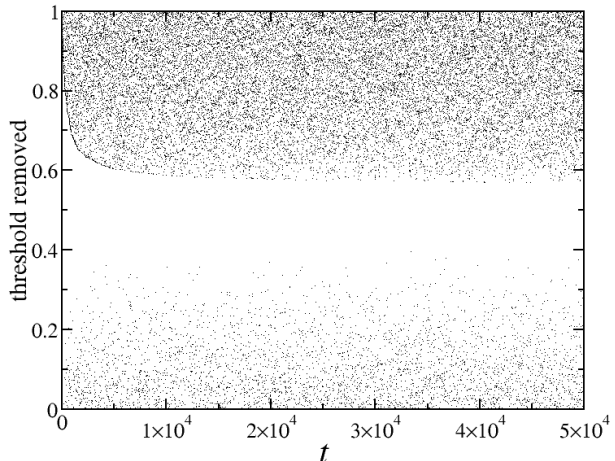


FIG. 1: For each time step, a data point indicates the threshold of the agent with the lowest payoff. The population is composed of 10^4 agents who interact in a one-dimensional lattice.

II. THE MODEL

A set of N agents are arranged in the nodes of a network. We set 1 unit the amount to be shared in each interaction. Each agent i is characterized by a threshold $T_i \in [0, 1]$: as responder it indicates the minimum amount he will accept; as proposer, it also defines the amount of money he will offer. This situation is usually named as *empathy* [30], and has been shown to enhance fairness in some situations in the ultimatum game [25, 26, 31]. Based on experimental evidence reported previously, we will assume that a fair offer-acceptance (threshold values around 50%) represents altruistic behavior.

The model runs as follows: at each time step all agents play with all their neighbors

synchronously. Thus for each interaction link between two neighboring agents (i, j) ,

- If the offer T_i is above the threshold of agent j , $T_i > T_j$, then the offer T_i is accepted: agent j increases his payoff by T_i while agent i 's payoff increases by $1 - T_i$. The payoff obtained by agent i (j) from the interaction with his neighbor j (i) is $\Pi_{ij} = 1 - T_i$ ($\Pi_{ji} = T_i$);
- Otherwise if the offer T_j is above the threshold of agent i , $T_j > T_i$, then the offer T_j is accepted: agent i 's payoff increases by T_j while agent j 's payoff increases by $1 - T_j$. The payoff obtained by agent i (j) from the interaction with his neighbor j (i) is $\Pi_{ij} = T_j$ ($\Pi_{ji} = 1 - T_j$).

The payoff obtained by agent i after interaction with the neighbors j in his neighborhood $\mathcal{V}(i)$ is thus $\Pi_i = \sum_{j \in \mathcal{V}(i)} \Pi_{ij}$. In the unlikely event that two neighboring agents thresholds are the same, one of the offers is selected and accepted at random. After each round, a selection rule is applied to the system: the agent with the lowest payoff in the population and its immediate neighbors, determined by the network, are replaced by new agents with randomly chosen thresholds [5]. We then let the system evolve resetting the payoffs of all agents to zero.

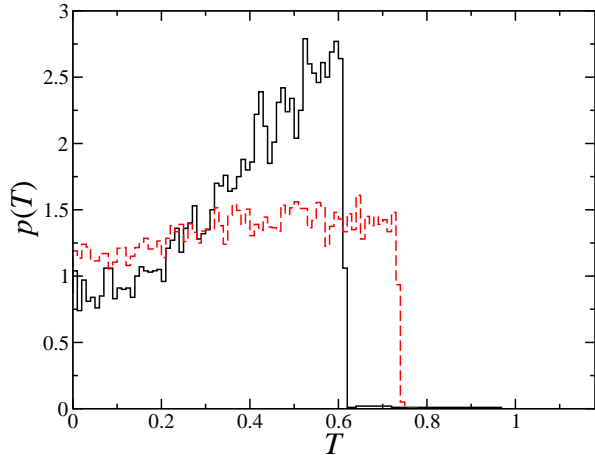


FIG. 2: Distribution of thresholds for 10^4 agents in a one-dimensional lattice (continuous line) and in a random network (dashed line) after 4×10^6 iterations. The dynamics selects threshold values below the critical threshold $T_c = 0.56$ in the one-dimensional lattice and $T_c = 0.88$ in the random network.

An alternative description of the model could set the interaction between two agents as a single event in which agent i acts as proposer and j as responder. However as long as the update is synchronous and every agent plays as proposer and responder with all its neighbors, this description and the dynamic rules (i)-(ii) are equivalent.

III. RESULTS

A. Single-scale interaction networks

Following previous studies of spatial games [20, 22, 32], we first consider a one-

dimensional lattice where each agent interacts with his two nearest neighbors. We have run simulations for populations in the range $N = 10^3$ to 10^4 agents, finding consistent results. The initial thresholds are randomly selected from a uniform distribution in the range $[0, 1]$. In Fig. 1 we display the threshold of the agent with the lowest payoff in the population at each time step. Agents with high and low thresholds are removed from the population. On the one hand, agents with high thresholds make large offers that are likely to be accepted by their neighbors, contributing to the neighbors payoff. However quite unlikely they receive large enough offers to be accepted due to their high threshold. This behavior can be illustrated calculating the expected payoff per interaction in a completely mixed population,

$$\langle \Pi(T) \rangle = T(1 - T) + \frac{1 - T^2}{2}. \quad (1)$$

In the limiting case of agents with threshold $T = 1$, they obtain on average a payoff close to 0. On the other hand, the opposite situation is observed for agents with low threshold: their offers are hardly accepted while they accept most of the offers they receive. In the limiting case of agents with threshold $T = 0$, they obtain on average a payoff close to $1/2$ per neighbor. Thus agents with low thresholds have in average a larger payoff than agents with high thresholds and are

able to survive. Although the previous argument has been obtained for a completely mixed population, we observe that it is still valid in the regular case (Fig. 2). Thus, after a transient, the distribution of thresholds reaches a stationary distribution. Thresholds above a critical value are removed from the population. For the one-dimensional lattice considered here, a critical threshold value is obtained $T_c = 0.56 \pm 0.01$. Below this critical value the distribution of thresholds is not uniform: it increases approaching the critical value. The payoff distribution also shows a nonuniform distribution: only values above a critical value $\Pi_c = 1.76$ are found, displaying a maximum at a value around $\Pi \simeq 2$.

The question we next address is whether the ultimatum model self-organizes in a critical state. In order to characterize the dynamics, we have measured the distribution of the distance Δx between two consecutive selection events, $C(\Delta x)$, and the first return time distribution, $P_f(t)$, the time elapsed between two selection events affecting the same agent. The results are plotted in Fig. 3. In both cases the tails of the distributions are well fitted by power-laws. For the spatial correlation

$$C(\Delta x) \sim \Delta x^{-\gamma}, \quad (2)$$

with $\gamma = 3.16 \pm 0.1$, and for the first return time

$$P_f(t) \sim t^{-\tau}, \quad (3)$$

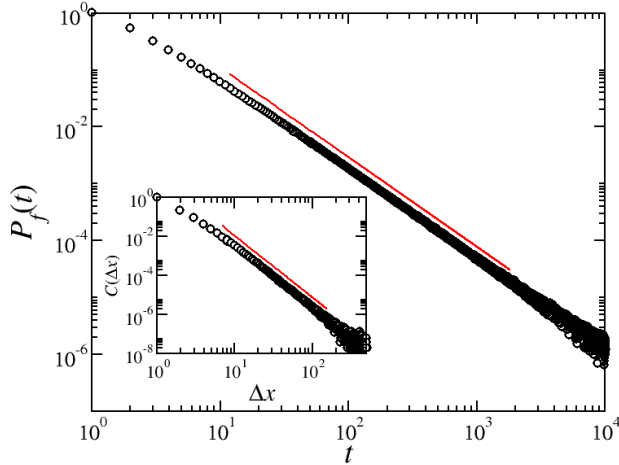


FIG. 3: First return time distribution for a system of 10^4 agents in a one-dimensional lattice. The solid line is a power-law fit with an exponent $\alpha = 1.57$. Inset: distribution of the distance Δx between two agents getting the lowest payoff consecutively. The solid line is a power-law fit with an exponent $\gamma = 3.16$.

with $\tau = 1.57$.

These results suggest that the system self-organizes in a critical state where the distribution of avalanches is also a power-law. The critical state would emerge despite the nonuniform distribution of thresholds (and payoffs). An avalanche is typically defined as follows: it starts when the lowest payoff gets larger than a preset value Π^* (close to the critical payoff), and stops when it drops below this value. The size, s , of an avalanche is the number of time steps it lasts. In Fig. 4, we show the distribution of avalanche sizes when we use a payoff $\Pi^* = 1.76$ as the indication of an avalanche. The probability dis-

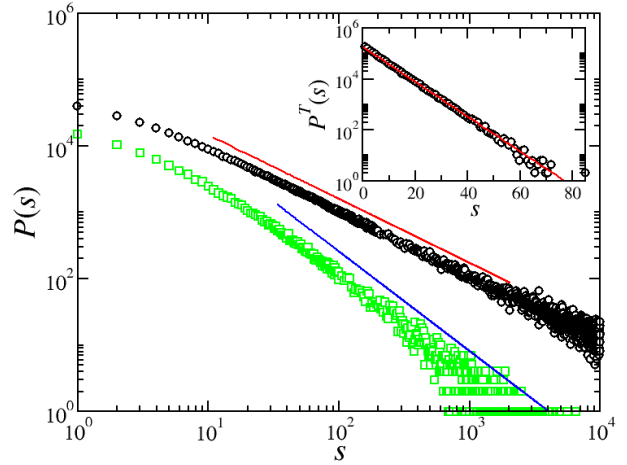


FIG. 4: Avalanche size distribution $P(s)$ a system of 10^4 agents in a one-dimensional lattice (circles) and in small-world networks (squares) with a rewiring probability $p = 0.15$. The solid lines is a power-law fit with an exponent $\alpha = 1.0$ and $\alpha = 1.5$, respectively. Inset: the avalanche size distribution $P^T(s)$ considering the thresholds instead of payoffs for the definition of an avalanche in a one-dimensional lattice. The solid line corresponds to the best exponential fit.

tribution displays a power-law decay

$$P(s) \sim s^{-\alpha}, \quad (4)$$

with an exponent $\alpha = 1.0$.

It is worth noting that if we had used the threshold value, T , as an indication of when an avalanche starts and stops, the distribution of avalanches would have decayed exponentially (see inset of Fig. 4). This behavior reflects that the thresholds being removed are not always above a critical value (as shown in Fig. 1): agents with low thresholds are re-

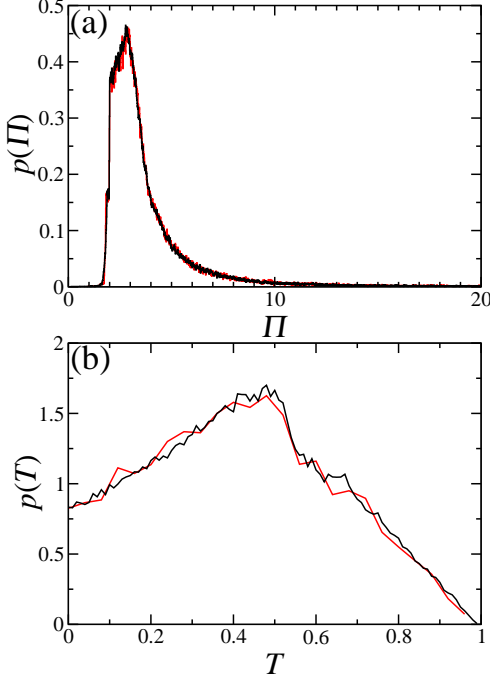


FIG. 5: (a) Distribution of payoffs and (b) distribution of thresholds for 10^4 agents in a scale-free network in the asymptotic state after 10^6 iterations. The distributions are averaged over 100 realizations.

moved often from the population. Thus, the fitness of an agent is given by its payoff.

Regular lattices are just a crude simplification of social and biological interaction. More realistic models of interaction networks include the small-world behavior: the average distance between agents in the network is similar to the one obtained in a random network, and the clustering, the fraction of neighbors of an agent that are also neighbors between them is large, as occurs in a regular lattice. We have performed simulations in

small-world networks generated by rewiring the links of a one-dimensional lattice, using the algorithm introduced in Ref. [21] in order to keep all the agents with the same number of links: With a probability p , two edges exchange their end nodes. The distribution of thresholds and payoff are similar to the one-dimensional lattice, as shown in Fig. 2. It can be seen that for the limiting case of a random network, the distribution of thresholds is broader, and has a higher critical threshold. In this case, the system also self-organizes in a critical state where the avalanche size distribution displays a power-law scaling. Similarly to the one-dimensional lattice, the avalanche size distribution (when considering the threshold as the dynamical variable) is not power-law, but exponential. For the small-world networks, the distribution of avalanche size is also power-law with an exponent that depends on the rewiring probability p . For instance, for a system of 10,000 agents we find an exponent $\alpha = 1.5$, for a value $p = 0.15$ (Fig. 4).

B. Scale-free interaction networks

In all the results presented so far, the network of interactions is such that the number of links of each node, its *degree*, is constant for all the agents. Beyond the small-world behavior, another important ingredient of in-

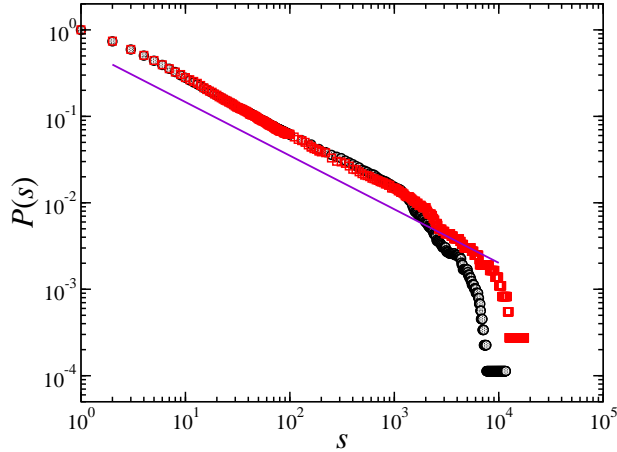


FIG. 6: The cumulative distribution of avalanches in a scale-free network with 10^4 (circles) and 2×10^4 agents. The distribution is well fitted by a power-law with an exponential cut-off. The solid line corresponds to a power-law fit, leading to an exponent $\alpha = 1.62$. The preset payoff that defines when an avalanche starts and ends is $\Pi^* = 1.77$. Averages are obtained over 100 realizations.

teraction networks is that they often display a scale-free degree distribution. We now turn into the study of the results of this model when the topology of interactions is not a regular one, but a scale-free one. As the model for the generation of the network, we used the Barabási-Albert algorithm [6, 7], generated as follows: starting from a fully connected network of size m , at time t a node is added, and attached to m existing nodes, where the probability to be attached to a node is proportional to its degree. This algorithm generates networks with a power-law degree dis-

tribution with an exponent $\gamma = 3$. We have fixed the value $m = 2$. Once the network is grown, it is kept fixed and the dynamics is played as indicated by rules (i) and (ii).

In Fig. 5(a) we plot the stationary distribution of payoffs in the population. There is a well defined critical payoff, below which the agents are removed. This critical value is $\Pi_c = 1.75 \pm 0.02$. For large payoffs, the distribution decays as a power-law with an exponent of 3, reflecting the decay of the degree distribution of the network. For the distribution of thresholds in the population (Fig. 5(b)), there is not cutoff in this distribution. All thresholds in the range $[0, 1]$ are present, with a maximum in the distribution around $T \simeq 0.5$. The distribution is highly asymmetric: it approaches zero for thresholds close to 1, while it reaches a finite fraction in the limit $T \rightarrow 0$. Thus, agents with low threshold values have more chances to survive. This is in agreement with the analytical argument in Eq. 1. In scale-free networks, the system also exhibits a power-law distribution of the size of the avalanches (Fig. 6). In this case, the payoff we set to define an avalanche is $\Pi^* = 1.77$ obtaining an exponent $\tau = 1.62$ for the a power-law scaling.

Why can in the scale-free network agents with high thresholds survive better than in a regular or random network? To address this

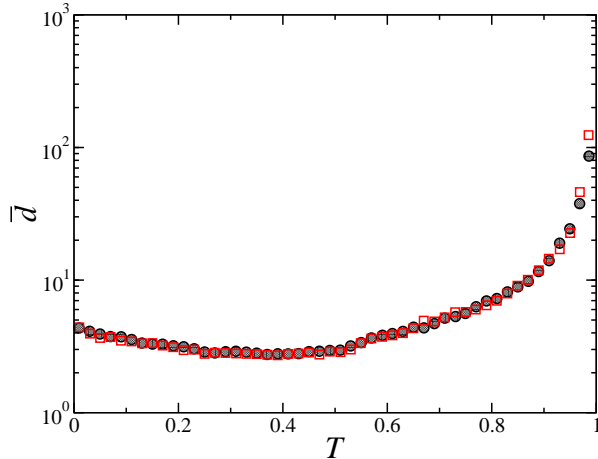


FIG. 7: Average degree \bar{d} of agents having a given threshold T when 10^4 agents interact in a scale-free network. Averages are obtained over 50 realizations.

question we have analyzed the average degree of the agents grouped according to their threshold, and the results are shown in Fig. 7. It can be seen that agents with high threshold values are more likely to survive if they are located at the hubs of the network. The reason for this is that they can accumulate payoff via interaction with a large number of agents.

It is worth noting that when the network is highly heterogeneous, for example when the degree distribution is scale-free, the dynamics depends on whether the payoff of each agent is normalized by its degree. For normalized payoffs in the scale-free networks described previously the critical threshold depends on the number of agents N . In the limit of large N the critical threshold tends to 1, in

contrast to the system size independent critical threshold reported previously, and the dynamics displays power-law distribution of avalanches when the threshold used to define an avalanche is chosen depending on N . A deeper analysis of the normalized payoff case goes beyond the scope of this paper.

IV. DISCUSSION AND CONCLUSIONS

How cooperation and altruism emerge among individuals is a withstanding question that has attracted much attention in the last years. Also the relevance of the complex social organization, and the concomitant network of interactions in supporting altruistic behavior is an open question [17, 18].

We have proposed an evolutionary ultimatum game with local interactions that self-organizes in a critical state. To analyze how social structure influences the degree of cooperation we have considered different topologies for the network of interactions. Assuming fairness as offer-acceptance around 50%, the amount of altruistic behavior in the Ultimatum Game is reflected in the distribution of thresholds in the population. In regular and single-scale networks, high thresholds leading to low payoffs are removed, while intermediate thresholds are selected in the populations. In scale-free networks, the dis-

tribution of thresholds displays a maximum around a value of 50%, decaying for lower and larger threshold values. Comparing with experimental results in small societies, both settings, the random and scale-free topologies, capture the experimental findings where offers around 50% are the most common. However, in the scale-free networks the distribution of thresholds covers all the range of threshold values decaying slowing from the maximum around 50%, in contrast to the sharp cutoff obtained in the random case. Thus, a hierarchical social structure may explain better the patterns of offer-acceptance found in some societies [13, 18].

From a dynamical point of view, in all the different complex networks we have analyzed, including regular lattices, small-world, random and scale-free networks, the distribution of avalanches displays a power-law scaling with an exponent that depends on network topology. This feature is typically a signature of self-organized criticality. Many complex systems in nature are found to display this phenomenon [4, 19]. They characterize long-range correlations in a system, similar to the behavior near a critical point in a phase transition. The model introduced here can be compared with other evolutionary models. The exponents that characterize the dynamics is the same as in the simple model of evolution proposed by Bak and Sneppen

(BS model) [5]. For the one-dimensional lattice, the exponents characterizing the first return time, spatial correlation and avalanche distribution for the ultimatum model introduced here are the same as for the BS-model; for random networks, the exponent of the avalanche size distributions corresponds to the mean-field exponent of the BS model. However, there is a crucial difference between the BS-model and the one introduced here: while in the BS-model the fitness is directly assigned to the agents randomly from a uniform distribution. In our model, the fitness is the outcome of the interactions and the distribution of thresholds is an emerging property of it.

The results presented here complement previous theoretical works on the emergence of cooperation. Among the most used theoretical games to study the emergence of cooperation in social sciences, the Prisoner's Dilemma is perhaps the most paradigmatic example. In this model, it has been shown that local interactions among agents can lead to a cooperative behavior in the so-called *spatial games* [22]. In evolutionary models, it was also found [20] that self-organized criticality can be present for this system. These results triggered the analysis of spatial games in different network topologies and strategies of the agents, aiming at uncovering the conditions under which cooperation can arise [32].

In particular scale-free networks have been shown to sustain cooperation [20]. Together with our results, hierarchical social structures, represented for instance by scale-free networks of interaction, suggest that primitive societies displaying this kind of interactions favored the emergence of altruistic behavior. To elucidate whether the interaction patterns facilitated altruism or altruistic behavior led to complex interaction patterns we need to incorporate more realistic ingredients to the models as for instance the possibility of removal and establishment of social ties depending on the outcome of the interaction [9]. Another open question is the evolution of empathy itself. In this work we have assumed that empathy has evolved before the thresholds are selected. However we expect that empathy will co-evolve simultaneously with the thresholds. Other extensions of the model could consider, for example, several repeated interactions between agents before selection. In this case, it could be argued that a repeated interaction scheme could allow for an adaptation of the threshold by the least successful agents. The interplay between adaptation and selection is an open question to be addressed in future works.

In summary, experiments have shown that altruistic behavior is common in human so-

cieties. Furthermore, it has been shown that social structure is a fundamental ingredient for understanding the distribution of sharing offers in the Ultimatum Game. We show that selection level together with local interactions can lead to a critical dynamics, where the precise degree of fair offer-acceptance depends on social structure. Recent developments on complex networks has allowed us to consider some simple models capturing basic features of networks of interaction. Our work emphasizes the importance of considering the social structure and calls for the development of more realistic networks models of social interaction to understand the interplay between individual behavior and with whom they interact.

Acknowledgments

We acknowledge Anxo Sánchez, and the Editor and the referees for providing valuable comments and insight. We acknowledge financial support from MEC (Spain) through project FISICOS (FIS2007-60327), and the European Commission through the NEST project EDEN (043251); CJT acknowledges SBF (Switzerland) through SER Project C05.0039.

- Rev. Mod. Phys.* **74**, 47–97 (2002).
- [2] Amaral, L.A.N., Scala, A., Barthélemy, M. and Stanley, H.E., Classes of small-world networks, *Proc. Natl. Acad. Sci. USA* **97**, 11149–11152 (2000).
- [3] Axelrod, R., *The Evolution of Cooperation* (Basic Books, 1984).
- [4] Bak, P., *How nature works* (Springer Verlag, 1996).
- [5] Bak, P. and Sneppen, K., Punctuated equilibrium and criticality in a simple model of evolution, *Phys. Rev. Lett.* **71**, 4083–4086 (1993).
- [6] Barabási, A.-L. and Albert, R., Emergence of Scaling in Random Networks, *Science* **286**, 509–512 (1999).
- [7] Barabási, A.-L., Albert, R. and Jeong, H., Mean-field theory for scale-free random networks, *Physica A* **272**, 173–187 (1999).
- [8] Darwin, C., *The descent of man, and selection in relation to sex*, (Murray, 1871).
- [9] Eguíluz, V.M., Zimmermann, M.G., Celasco, C.J. and San Miguel, M., Cooperation and emergence of role differentiation in the dynamics of social networks, *Am. J. Sociology* **110**, 977–1008 (2005).
- [10] Fehr, E. and Gächter, S., Altruistic punishment in humans, *Nature* **415**, 137–140 (2002).
- [11] Gould, S.J., *The structure of evolutionary theory* (Harvard University Press, 2002).
- [12] Güth, W. and Tietze, R., Ultimatum bargaining behavior, a survey and comparison of experimental results, *J. Econ. Psychol.* **11**, 56–90 (1990).
- [13] Hamilton, M.J., Milne, B.T., Walker, R.S., Burger, O. and Brown, J.H., The complex structure of hunter-gatherer social networks, *Proc. R. Soc. B* **274**, 2195–2202 (2007).
- [14] Hauert, C., Cooperation, collectives formation and specialization, *Adv. Complex Sys.* **9**, 315–335 (2006a).
- [15] Hauert, C., Spatial effects in social dilemmas, *J. theor. Biol.* **240**, 627–636 (2006b).
- [16] Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H. and McElreath, R., In Search of Homo Economicus: Behavioral Experiments in 15 Small-Scale Societies, *Am. Econ. Rev.* **91**, 73–78 (2001).
- [17] Henrich, J. et al., “Economic man” in cross-cultural perspective: behavioral experiments in 15 small-scale societies, *Behav. and Brain Sci.* **28**, 795–815 (2005).
- [18] Henrich, J. et al., Costly punishment across human societies, *Science* **312**, 1767–1770 (2006).
- [19] Jensen, H.J., *Self-organized criticality: emergent complex behavior in physical and biological systems* (Cambridge University Press, 1998).
- [20] Killingback, T. and Doebeli, M., Self-

- organized criticality in spatial evolutionary game theory, *J. theor. Biol.* **191**, 335–340 (1998).
- [21] Maslov, S., Sneppen, K. and Alon, U., in *Handbook of graphs and networks. From the genome to the internet.*, (Wiley VCH and Co. Weinheim, 2003).
- [22] Nowak, M.A. and May, R.M., Evolutionary games and spatial chaos, *Nature* **359**, 826–829 (1992).
- [23] Onnela, J.P., Saramäki, J., Hyvönen, J., Szabó, G., Lazer, D., Kaski, K., Kertész, J. and Barabási, A.-L., A.L., Structure and tie strengths in mobile communication networks, *Proc. Natl. Acad. Sci. USA* **104**, 7332–7336 (2007).
- [24] Oosterbeek, H., Sloof, R. and van de Kuilen, G., Differences in ultimatum game experiments: Evidence from a meta-analysis, *Exp. Economics* **7**, 171–188 (2004).
- [25] Page, K.M. and Nowak, M.A., A generalized adaptive dynamics framework can describe the evolutionary ultimatum game, *J. theor. Biol.* **209**, 173–179 (2000).
- [26] Page, K.M. and Nowak, M.A., Empathy leads to fairness, *Bull. Math. Biol.* **64**, 1101–1116 (2002).
- [27] Page, K.M., Nowak, M.A., Sigmund, K., The spatial ultimatum game, *Proc. R. Soc. Lond. B* **267**, 2177–2182 (2000).
- [28] Palla, G., Barabási, A.-L. and Vicsek, T., Quantifying social group evolution, *Nature* **446**, 664–667 (2007).
- [29] Pennisi, E., How Did Cooperative Behavior Evolve?, *Science* **309**, 93 (2005).
- [30] Preston, S.D. and de Waal, F.B.M., Empathy: its ultimate and proximate bases, *Behav. Brain Sci.* **25**, 1–72 (2002).
- [31] Sánchez, A. and Cuesta, J.A., Altruism may arise from individual selection, *J. theor. Biol.* **235**, 233–240 (2005).
- [32] Santos, F.C., Pacheco, J.M. and Lenaerts, T., Evolutionary dynamics of social dilemmas in structured heterogeneous populations, *Proc. Natl. Acad. Sci. USA* **103**, 3490–3494 (2006).
- [33] Szabó, G. and Fáth, G., Evolutionary games on graphs, *Phys. Rep.* **446**, 97–216 (2007).